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DETERMINANTS OF THE DISTRIBUTION OF APPLE SNAILS IN HONG KONG TWO DECADES AFTER THEIR INITIAL INVASION

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ABSTRACT

This study examined the relative importance of environmental factors and geographic isolation on the distribution of apple snails in Hong Kong two decades after their invasion from South America. A survey of 61 sites was conducted to collect apple snails and measure 18 environmental parameters known to influence mollusk distribution. Identification of specimens collected in our study was aided by analysis of DNA sequences, and all apple snails collected in Hong Kong were identified as *Pomacea canaliculata*. Since its initial introduction in the early 1980s, the distribution of this invasive snail has only expanded slightly. Principal component analysis showed that the environmental characteristics of the study sites varied with habitat. Streams were quite homogenous in chemical characteristics and contained little dissolved minerals, whereas ponds, abandoned wet farmlands and drainage channels all showed great variations in nutrient loading. Discriminant function analysis (DFA) revealed that the inhabited sites typically had high levels of phosphate and alkalinity, but the snail was also occasionally found in streams where dissolved ion concentrations and nutrient levels were low. Most of the inhabitable wetlands in New Territories have already been occupied by *P. canaliculata*. Because of its unsuitable hydrology, Hong Kong Island remains uninhabited by this species. Lantau Island has habitable sites for this species, and thus is susceptible for invasion in the future.

Key words: Ampullariidae, *Pomacea*, hydrology, nutrient, distribution.

INTRODUCTION

Apple snails *Pomacea* spp. (Gastropoda: Ampullariidae) are native to the freshwater habitats of South America (Martín et al., 2001; Cowie et al., 2006). They were first introduced into Asia as a delicacy and as a potential food crop in the early 1980s, but soon escaped aquaculture and established wild populations in various countries (Chang, 1985; Mochida, 1991; Halwart, 1994; Naylor, 1996; Cowie, 2002; Teo, 2004). *Pomacea* spp. are omnivorous, feeding on microorganisms and detritus on surface biofilm, eggs and juveniles of other snails, animal carrion, and macrophytes, with the latter being predominant (Cowie, 2002). Their ability to consume macrophytes has made them important pests in Asia's rice farming areas and non-agricultural wetlands (Carlsson et al., 2004; Carlsson & Lacoursière, 2005).

Few quantitative assessments of the habitat of apple snails have been conducted; therefore factors regulating their distribution are poorly understood. In its home range of Buenos Aires Province, Argentina, high alkalinity has been implicated as a possible chemical barrier against the expansion of *Pomacea canaliculata* to the western region, whereas mountains likely form a geographic barrier against its southern expansion (Martín et al., 2001). However, the chemical characteristics of the surface water in Hong Kong are very different from those in Argentina. For instance, mean conductivity in its home range (3.5 mS cm^{-1}) is 48 to 10 times of that in Hong Kong (from 0.07 mS cm^{-1} in streams to 0.35 mS cm^{-1} in flooded furrows; data from Yipp, 1990). Thus, the conclusions from Martín et al. (2001), especially those regarding how high alkalinity limiting apple snail distribution, may not be applicable to the situation in Hong Kong.

Apple snails invaded Hong Kong in the early 1980s. The only survey of apple snails was conducted in 1988 by Yipp et al. (1991), who reported two species – *P. maculata* and *P.*

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lineata, both likely misidentifications of *P. canaliculata* – from the vegetable farming areas in the northern New Territories bordering Guangdong Province, China. They also analyzed the water samples from the inhabited sites, and found them to have high nutrient (nitrogen and phosphorus) contents and conductivity. But they did not analyze samples from the non-inhabited sites, considering that these sites remained uncolonized probably due to geographical isolation rather than unsuitable hydrology. The small land area (1,104 km^2) with various aquatic habitats (i.e., streams, drainage channels, ponds, and abandoned wet farmlands) in Hong Kong and the length of time (two decades) since the initial invasion by apple snails provide an ideal opportunity to examine the relative contribution of habitat requirements and geographic barriers in determining the distribution of this invasive species. We hypothesize that the current distribution pattern of apple snails in Hong Kong should reflect their habitat requirements, rather than geographic isolation. We surveyed various freshwater habitats and determined a number of water and sedimentary parameters that are known to influence the distribution of mollusks (Green, 1971; Lodge et al., 1987; Dillon, 2001). Our goals were to update the species identity and distribution range of apple snails in Hong Kong and to determine environmental parameters that may have influenced their distribution. The information may allow us to predict wetland habitats that are suitable for the colonization of apple snails in this region, and possibly inform invasions in other regions.

MATERIALS AND METHODS

Study Area

Geographically, Hong Kong can be divided into four larger areas – New Territories, Kowloon, Hong Kong Island and Lantau Island – and 261 smaller outlying islands (Fig. 1). Kowloon is a highly urbanized area with no suitable habitat for aquatic wildlife. New Territories can be divided into a relatively flat northern part and a relatively hilly southern part, although there is no distinct boundary between the two. Hong Kong Island is connected with Kowloon by two underground tunnels, whereas Lantau and Kowloon are linked by two bridges. Traditionally, agriculture was practiced in these three areas, with rice as the staple crop. However, due to rapid urbanization, active agriculture can be seen only in northern New Territories, with vegetable and flower production accounting for about 97% of the total value of local crop production (AFCD, 2007).

Sampling and Sample Analysis

Our preliminary field trips to a number of sites showed that, during winter, few apple snails reproduced, and the population size was so small that it was difficult to find any individuals. Sampling was thus conducted during summer 2006 when apple snail population densities were high and their egg clutches were easy to see. Sixty-one sites across the rural areas of Hong Kong were chosen (Fig. 1). Some of these were identical to those in Yipp et al. (1991). Others were determined by checking a local map showing the major freshwater habitats. Overall, there were more sites in northern New Territories where there were more freshwater habitats. In each site, searches for apple snails and their egg clutches were performed by the same two people (K. L. Kwong & P. K. Wong). These were done by checking for up to 250 m of the shore of each water body for the presence of the colorful egg clutches on emergent vegetation or the bank of the site, as well as living apple snails among submerged vegetation, on the mud surface, or under stones (Martín et al., 2001). A site was considered uninhabited when no living apple snails or their egg clutches were found. When apple snails were present, the most morphologically distinct individuals were collected, and a selection of these individuals were later sent to Robert Cowie and Kenneth Hayes of the University of Hawaii for species identification using a portion of the mitochondrial cytochrome *c* oxidase subunit I sequence (COI), as described in Cowie et al. (2006).

Several environmental parameters that are known to affect mollusk distribution were determined. In each site, water depth was determined by inserting an extensible fishing rod into the middle of the water body until it touched the bottom, and measuring the portion of submerged rod using a tape measure. Flow rate was measured with a JDC Flowatch meter. Turbidity was measured with an Orion AQ4500 turbidometer. Dissolved oxygen (DO), pH, and conductivity were measured with an Orion 1230 multiparameter meter. Two water samples (1L) were taken with P.V.C. bottles

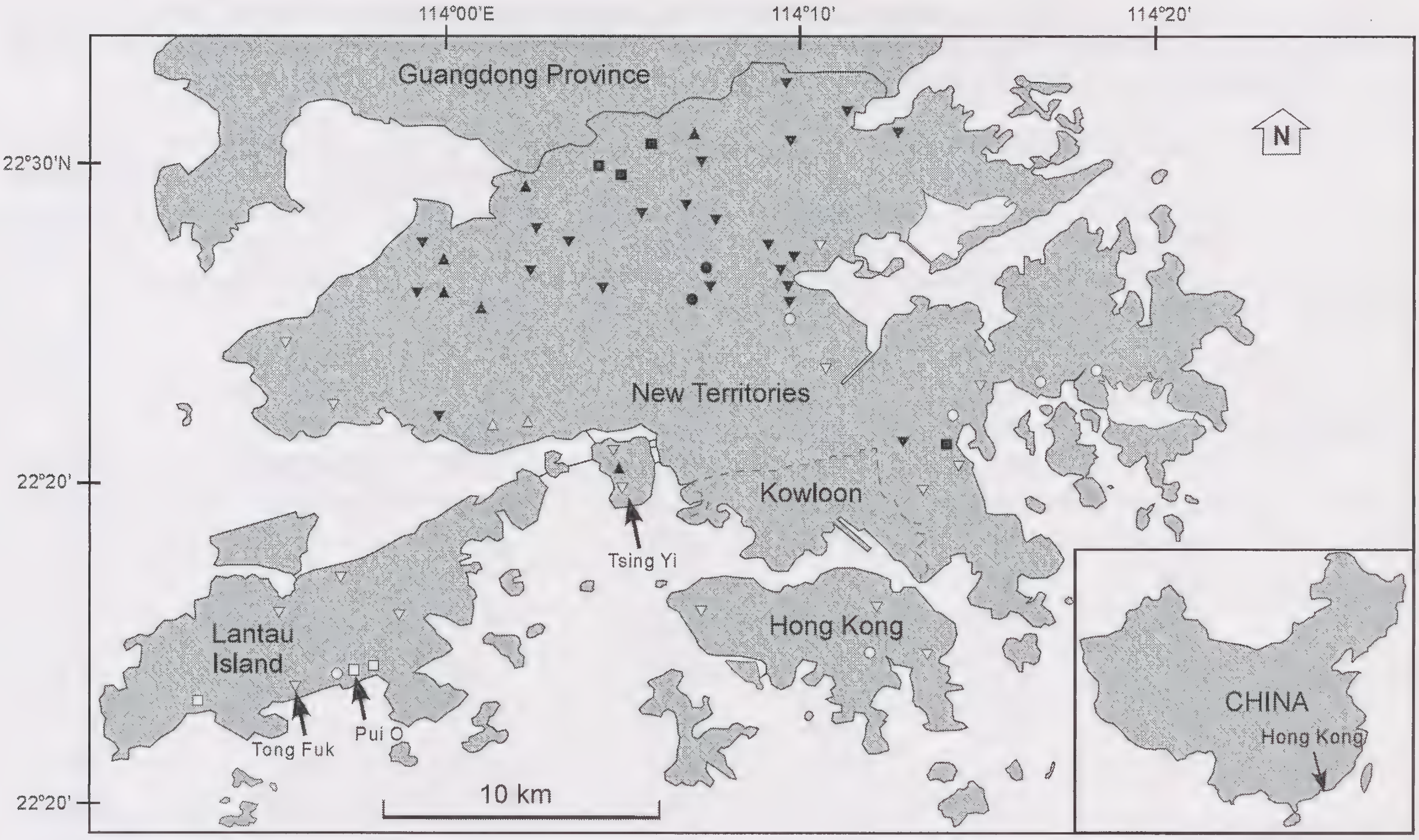

FIG. 1. Map of Hong Kong showing the sampling sites, their habitat type (○ – stream, ∇ – drainage channel, Δ – pond, □ – abandoned wet farmland) and the presence (filled symbol) or absence (open symbol) of *Pomacea canaliculata*. Inset: A map of China showing the location of Hong Kong.

and stored at 4°C in a portable cooler. Upon return to the laboratory, water samples were filtered through a 0.45 µm Gelman 66191 membrane filter. Subsamples were kept at appropriate temperature with respect to the chemical parameter to be analyzed. All chemical parameters, except nitrate and nitrite, were measured using standard methods (Eaton et al., 2005). Total alkalinity was determined by titration with sulphuric acid (Method 2320 B). Several captions were measured with a Varian Spectr AA-20 atomic absorption spectrometer (Method 3111 B for Mg^{2+}, K^+, Na^+ and Fe^{2+} and Method 3111 D for Ca^{2+}). Total phosphate was measured with the ascorbic acid method (Method 4500P E) and ammonia with the phenate method (Method 4500NH_3 F). Sulphate content was measured with the turbidimetric method (Method 4500-SO_4^{2-} E). Nitrate and nitrite were measured with Hach low range nitrate (Model NI-14, Cat No. 14161-00) and nitrite (Model NI-15, Cat No. 21820-00) test kits. In sites with a soft substratum, two surface (0–5 cm) sediment samples (approximately 0.5 kg) were collected for analysis of the particle size and organic matter. Subsamples were treated with hydrogen peroxide and sodium pyrophosphate, wet-sieved with an Octagon digital shaker into six graded fractions (2 mm to < 0.063 mm) and oven-dried (50°C) to constant weight. Mean particle size and inclusive graphic standard deviation were then determined. The remaining samples were ignited at 550°C to constant weight to determine the content of organic matter.

Data Analysis

For each site we calculated the mean value of each chemical and physical parameter to be used in statistical analysis. Sedimentary properties were not used because the data were not available from a number of sites where the bottom was concrete or rock. Turbidity data were not included because they were affected by instantaneous human disturbance, such as drainage of vegetable gardens, in some of the survey sites. Conductivity data were not included because they were a combined measure of inorganic ions. Ammonia, nitrite and nitrate values were pooled to give an overall estimate of total inorganic nitrogen. Except for pH, the data were subjected to log ($x + 1$) transformation. All statistical analyses were conducted using SPSS ver. 11 for Windows (SPSS, Inc.). Principal components

TABLE 1. The incidence of *Pomacea canaliculata* in four types of habitats surveyed, and the corresponding environmental parameters of each type of habitat. Each datum is mean (Standard deviation) of all sites of each habitat type.

	All sites (n = 61)	Stream (n = 8)	Drainage channel (n = 38)	Pond (n = 8)	Abandoned wet farmland (n = 7)
No. sites with *P. canaliculata*	34	2	22	6	4
% sites with *P. canaliculata*	55.7	25.0	57.9	75.0	57.1
Depth (cm)	33.9	29.4	27.0	87.5	15.0
	(33.7)	(14.5)	(12.0)	(69.2)	(6.5)
pH	6.7	6.4	6.9	6.4	6.5
	(0.7)	(0.4)	(0.6)	(0.8)	(0.4)
DO (mg l^{-1})	4.3	5.7	4.4	3.4	3.5
	(2.0)	(2.0)	(1.7)	(2.6)	(2.5)
Turbidity (NTU)	10.8	5.0	11.2	8.1	18.2
	(17.0)	(5.0)	(19.9)	(7.0)	(15.3)
Flow rate (cm s^{-1})	9.4	13.1	12.7	0.0	0.0
	(11.9)	(11.6)	(13.3)	(0.0)	(0.0)
Alkalinity (mg $CaCO_3$ l^{-1})	41.9	9.8	41.2	58.9	63.1
	(41.6)	(7.6)	(39.5)	(56.9)	(39.0)
Calcium (mg l^{-1})	23.8	11.0	23.9	33.2	27.7
	(16.4)	(2.6)	(16.0)	(21.3)	(14.6)
Magnesium (mg l^{-1})	8.1	6.2	7.1	15.9	6.4
	(7.7)	(1.4)	(2.5)	(19.5)	(3.2)
Potassium (mg l^{-1})	5.7	3.3	5.2	9.7	6.6
	(4.8)	(0.6)	(2.6)	(10.5)	(5.1)
Sodium (mg l^{-1})	54.3	45.2	49.7	91.6	47.5
	(41.7)	(12.2)	(17.8)	(103.9)	(22.9)
Iron (mg l^{-1})	0.7	0.3	0.6	0.4	1.7
	(1.0)	(0.4)	(0.8)	(0.1)	(2.1)
Sulphate (mg l^{-1})	17.1	5.7	15.2	30.8	24.8
	(25.9)	(5.2)	(22.7)	(34.4)	(40.2)
Inorganic nitrogen (mg l^{-1})	1.2	0.2	1.5	1.3	0.4
	(2.3)	(0.5)	(2.8)	(1.8)	(0.3)
Total phosphate (mg l^{-1})	0.9	0.1	1.0	1.0	1.7
	(1.4)	(0.2)	(1.3)	(1.1)	(2.5)
Conductivity (µS cm^{-1})	169.2	49.3	172.0	239.3	211.1
	(130.0)	(15.9)	(113.8)	(173.1)	(161.1)
Mean particle size (mm)	0.3	0.5	0.4	0.1	0.1
	(0.3)	(0.2)	(0.3)	(0.1)	(0.1)
Sorting coefficient	1.9	1.5	1.8	2.4	1.9
	(0.6)	(0.1)	(0.6)	(1.1)	(0.6)
% organic matter	3.7	1.6	3.3	7.4	5.4
	(3.9)	(0.8)	(4.1)	(3.8)	(2.9)

analysis (PCA) was performed on the correlation matrix to characterize the chemical and physical characteristics of the water in study area. To simplify the data structure and thus aid in the interpretation of the results, the component loadings were rotated using the

TABLE 2. Results of principal components analysis of water quality parameters (n = 59) showing Varimax rotated component loadings, eigen values, and percentage of variance explained.

Variable	PC 1	PC 2	PC 3	PC 4
Depth	-0.328	0.351	-0.381	0.495
pH	0.488	-0.071	0.732	0.127
DO	-0.376	-0.118	0.779	0.060
Flow rate	-0.282	0.470	0.117	0.395
Alkalinity	0.792	-0.340	-0.048	0.254
Calcium	0.919	-0.114	0.077	0.024
Magnesium	0.558	0.665	-0.108	-0.272
Potassium	0.825	-0.027	0.057	0.080
Sodium	0.414	0.771	-0.049	-0.396
Iron	0.393	-0.544	-0.289	-0.086
Inorganic nitrogen	0.545	0.326	-0.042	0.564
Total phosphate	0.601	-0.002	-0.016	-0.006
Sulphate	0.768	0.091	-0.013	-0.048
Eigen value	4.61	1.94	1.41	1.05
Cumulative % variation	35.4	50.3	61.2	69.3

Varimax method (Norušis, 2005). Stepwise discriminant function analysis (DFA) was conducted to determine the major hydrological parameters in distinguishing sites that were inhabited or uninhabited by apple snails. Parameters were entered until no additional parameter would significantly increase the discriminating power of the function. To determine whether the absence of apple snails in Lantau and Hong Kong Islands was due to unsuitable chemical and physical characteristics of the water, we used data from the New Territories and Tsing Yi to build up a discriminant function, and data from Lantau and Hong Kong Islands to cross-validate the result.

RESULTS

Species Identity and Distribution of Apple Snails

Morphologically, the collected apple snails showed two color variants – one with a brown shell and brown head-foot, and another with a yellow shell and yellow head-foot. The brown variant was dominant, accounting for over 95% of the total individuals found. The yellow variant was rarely found. Based on mitochondrial COI gene sequences of the 16 most morphologically distinct specimens, R. Cowie and K. Hayes determined our samples to be *P. canaliculata*. Overall, apple snails were found in 34 of the 61 surveyed sites (Table 1). They were very common in northern New Territories, sporadically distributed in southern New Territories and Tsing Yi Island, and not present in Lantau or Hong Kong Islands (Fig. 1). The surveyed sites could be divided into streams, drainage channels, ponds and abandoned wet farmlands. Apple snails were found in all of the four habitat types, but their incidence differed, ranging from 25% in streams to 75% in ponds.

Environmental Characteristics of Surveyed Sites

The environmental parameters differed substantially among the four types of habitats (Table 1). In general, the streams were characterized by coarse sediment, high DO, and flow rate, but low turbidity, conductivity, alkalinity, positive ions and nutrients. The ponds usually had high alkalinity, conductivity, calcium, magnesium, sodium and sulphate. The water quality values of the drainage channels typically lay between those of the streams and ponds. The abandoned wet farmlands were similar to the ponds in a number of water quality parameters, with notable exceptions of shallowness and extremely low levels of DO in a number of sites.

Principal components analysis reduced the variability of the original 13 parameters into four components that had an eigen value greater than 1, which in total captured 69.3% of the total variability (Table 2). The analysis

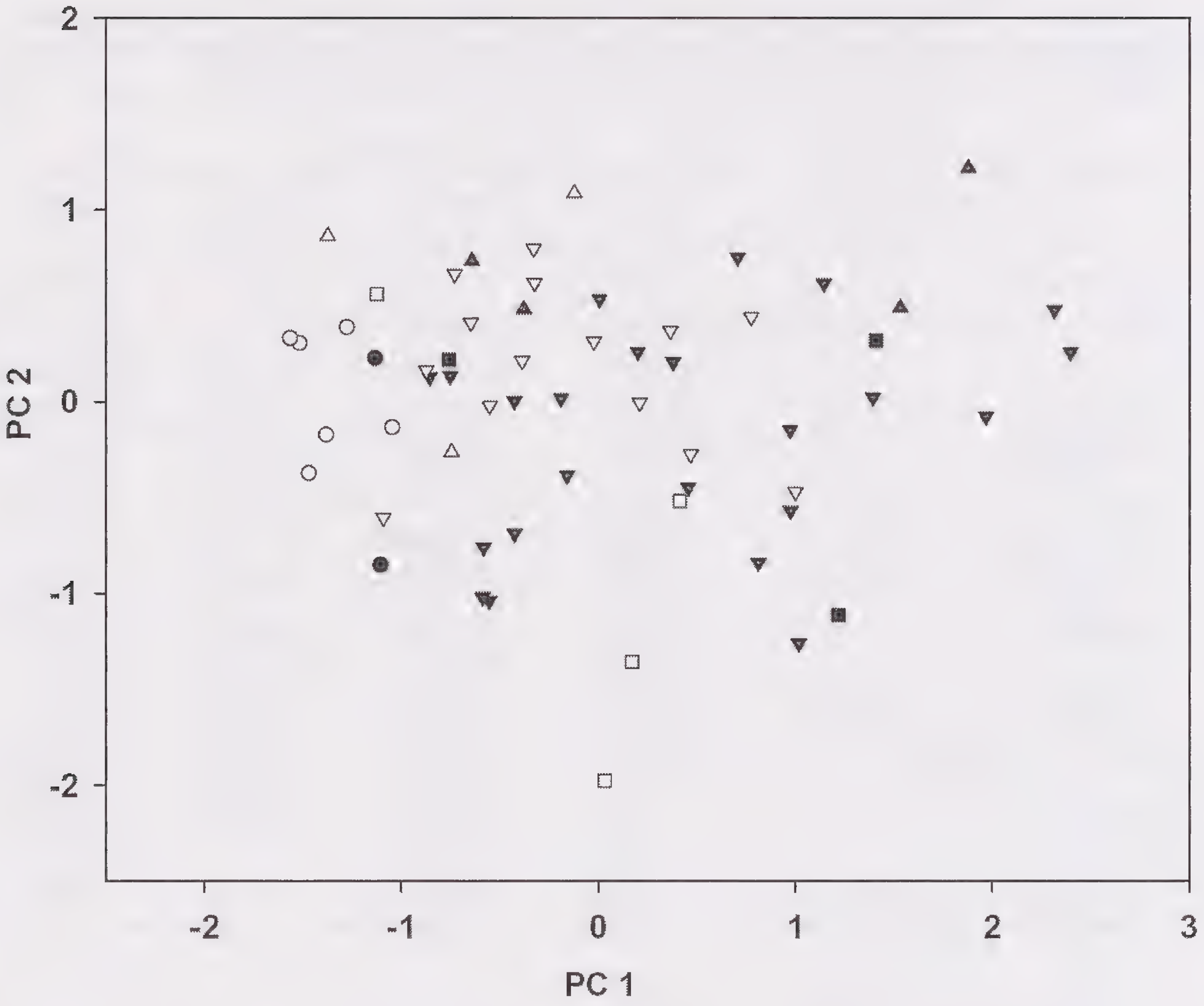

FIG. 2. A 2-D plot of the principal component loadings based on 13 environmental parameters of 59 surveyed sites. Two of the 61 sites were excluded because one had extremely high level of sodium, and another had extremely low levels of dissolved minerals. Including them would have distorted the distribution pattern of other sites along PC 2. Different symbols were used to show the four habitat types (O – stream, ∇ – drainage channel, Δ – pond, □ – abandoned wet farmland) and the presence (filled symbol) or absence (open symbol) of *Pomacea canaliculata*. PC 1 mainly represents nutrient loading and water hardness whereas PC 2 is largely dominated by sodium and magnesium.

resulted in a Kaiser-Meyer-Oklin value of 0.713, indicating its adequacy in representing the variability of the original data. The scores of the first two components were presented as a 2-D plot (Fig. 2). Along the PC 1 most parameters have a positive loading, especially calcium, potassium, alkalinity, and sulphate. Dissolved oxygen, depth and flow rate had a weak and opposite trend (Fig. 2, Table 2). The PC 2 was largely dominated by sodium and magnesium, both have a positive loading, while iron and alkalinity had a weak opposite trend. Figure 2 also illustrates the relationship between habitat type and hydrology. The stream sites are clustered, with negative loadings on PC 1 and low loadings on PC 2, indicating low nutrient loading in these sites and high similarities in chemical and physical characteristics of the water among them. The pond sites are spread widely across PC 1, indicating high variation in nutrient loading among them, but in general have a positive loading on PC 2, reflecting higher salinity, magnesium concentrations and depth. The abandoned wet farmlands are also spread widely across PC 1, but on PC 2 they typically have low values. Most of the drainage channel sites lay between the pond and wet farmland sites on PC 2. Dissolved oxygen and pH were the major determinants of PC 3, and inorganic nitrogen and depth were the major determinant of PC 4. These two components, however, only explained 19% of the total variability.

Distribution of Apple Snails in Relation to Water Quality

The stepwise DFA of chemical and physical parameters of the New Territories and Tsing Yi sites resulted in total phosphate and alkalinity being selected as the parameters to discriminate between sites with and without apple snails. The correlation between canonical discriminate function and total phosphate and alkalinity was 0.798 and 0.723, respectively. The results (canonical correlation = 0.501, Wilks' λ = 0.749, χ^2 = 12.692, *P* = 0.002) showed that, of the 47 sites used, DFA was able to correctly classify 74% of the cases. The percentage of correctly classified cases was higher for the prediction of their absence (80%) than that for their presence (69%). High total phosphate and alkalinity levels characterized sites that were inhabited by *P. canaliculata*, whereas low levels of the two parameters characterized the uninhabited sites. When the discriminant function was applied to cross-validate the 12 sites from Hong Kong and Lantau Islands, ten sites were correctly classified as uninhabited, while two sites were misclassified as inhabited.

DISCUSSION

Environmental Characteristics of Surveyed Sites

The surveyed wetland habitats were broadly categorized into streams, drainage channels, ponds and abandoned wet farmlands (i.e., rice paddies or vegetable farms), representing the typical freshwater wetland habitats in Hong Kong. A comparison showed substantial differences in chemical and physical parameters among these different habitats, as well as within the same type of habitat, except for streams, where the hydrology was uniform (Fig. 1, Table 1). Such a situation can be explained by the facts that igneous rock underlying most parts of Hong Kong is relatively homogenous in chemical composition and streams are relatively unaffected by human activities (Dudgeon & Corlett, 2004); the ponds and drainage channels are affected by nutrient enrichment from vegetable and flower production or poultry and pig farming, as well as periodic flooding during the summer monsoon. Some abandoned wet farmlands are anoxic because of the high organic content in the soil and poor drainage. In general, PCA results on hydrological parameters (Fig. 2, Table 2) can be explained by the relative intensity of human activities and distance from the coast. PC 1 is an assessment of eutrophication. PC 2 is a measure of salinity and magnesium. Overall, the 2-D PCA plot gives a good visual presentation of the chemical and physical characteristics of the study area (Fig 2).

Species Identity and Distribution of Apple Snails

Yipp et al. (1991) reported the presence of two species, *Ampullaria gigas* (Spix, 1827) and *Ampullaria levior* (G. B. Sowerby III, 1909). According to Cowie (1997), *Ampullaria* is a junior synonym of *Pomacea*. According to Alderson (1925), *P. levior* is a junior synonym of *P. lineata*, and *P. gigas* is a junior synonym of *P. maculata*. The molecular results of Cowie et al. (2006) showed that only four *Pomacea* species have been introduced into Asia: *P. canaliculata* and *P. insularum* to many Asian countries, *P. diffusa* to Sri Lanka, and *P. scalaris* to Taiwan. *Pomacea lineata* is very similar to *P. canaliculata* in shell morphology, body color, and egg clutch (Cazzaniga, 2002). Molecular sequencing of some of our selected specimens showing the greatest morphological variations by R. Cowie and K. Hayes clearly revealed the identity of the specimens throughout Hong Kong to be *P. canaliculata*. It is therefore very likely that the apple snail reported as *A. levior* by Yipp et al. (1991) and as *P. lineata* by Lam (1994) and Dudgeon & Corlett (2004) from Hong Kong is *P. canaliculata*. *Pomacea maculata*, reported by Yipp et al. (1991) as *P. gigas*, might be a misidentification of *P. canaliculata* that had a larger and thinner shell when compared with normal sized individuals. In fact, a subspecies of *P. canaliculata* with these conchological characteristics was described by Hylton-Scott (1948) from a $CaCO_3$ poor environment. But it is now well-known that *P. canaliculata* exhibits plasticity in shell thickness and shape (Cazzaniga, 2002; Estebenet & Martín, 2003; Cowie et al., 2006).

In the first survey of apple snails in Hong Kong conducted in 1988 (Yip et al., 1991), shortly after their introduction, they were confined to the northern New Territories. In this survey, we confirmed that northern New Territories is still their center of distribution (Fig. 1). As pointed out by Yipp et al. (1991), the frequent occurrence of apple snails in the northern New Territories was probably due to the relatively flat terrain with an extensive network of drainage channels plus seasonal monsoons, which must have facilitated its dispersion. In southern New Territories and Tsing Yi Island, where Yipp and her colleagues did not find apple snails, we only recorded isolated *P. canaliculata* populations. Such a pattern indicates a slow expansion of distribution range by the apple snails, given that it has been two decades since its initial introduction and the total area of New Territories is only 796 km^2.

Can We Predict the Suitability of a Site for Apple Snails Based on Water Characteristics?

Factors affecting the distribution of freshwater gastropods can be broadly classified into biological (i.e., food, competition, predation), chemical and physical (i.e., calcium, salinity, flooding, current speed, substratum, temperature, desiccation, geographic barrier), or cultural (i.e., aquarium trade) (Lodge et al., 1987; Dillon, 2001; Cowie, 2002). Limiting factors for the distribution of *P. canaliculata* are in general considered to be chemical and physical, because there is no evidence to show that competition or predation can effectively eradicate this species (Cowie, 2002; Pizani et al., 2005; Yusa et al., 2006a).

Due to the limited number of quantitative studies of the habitats of *P. canaliculata*, there is no sufficient information to determine the importance of chemical or physical factors in regulating its distribution and range expansion. Temperature is often a limiting factor for the northern distribution of tropical and subtropical species, and in fact the abundance of apple snail populations in Hong Kong is very low in winter months (Cha, 1989). But it is obviously not a limiting factor for its distribution in Hong Kong, given that the mean air temperature in the coldest month (January) is as high as 15.8°C, and this species can survive through the winter in some isolated locations in Japan where the monthly temperature can drop to 8.3°C (Ito, 2002). Although during the winter *P. canaliculata* usually suffer from high mortality, especially in drained fields, individuals living in aquatic environments may acquire cold hardiness, and the population may explode when water temperature increases in the spring (Yusa et al., 2006b; Wada & Matsukura, 2007). Salinity has been generally considered a limiting factor for the distribution of freshwater biota. However, it should not be a limiting factor for our surveyed sites, because we recorded *P. canaliculata* in a site with sodium concentration reaching as high as 0.35 g l^{-1}. Martín et al. (2001) examined the contribution of a number of chemical and physical factors to the distribution of *P. canaliculata* in its home range in Buenos Aires Province, Argentina. They noted that chemical characteristics of the water (saline, alkaline waters) formed a physiological barrier for the expansion of apple snails to the inland, western part of their study area, where the mean annual precipitation was only as low as 600 mm, whereas mountains formed a geographic barrier for its southern expansion.

Our DFA analysis revealed that water of high total phosphate and alkalinity was characteristic of sites inhabited by *P. canaliculata* in Hong Kong, which is different from the situation in its home range. The percentage of correctly classified cases for the absence of apple snails was high (80%). Of the 15 sites where apple snails were absent, only three were misclassified. This indicates that chemical and physical characteristics of the water can be a reasonably good predictor of apple snail absence, probably reflecting that most inhabitable sites have already been colonized. The three exceptions were all drainage channels, where the bottom and walls were lined with cement and water velocity can be very high during the wet season, a condition discouraging the establishment of apple snail populations. High current velocity also discouraged the accumulation of mud, which might be a refuge for apple snails. The lower percentage of correctly classified cases for the presence of apple snails (69%) reflected the fact that apple snails were found in ten sites of apparent unsuitable hydrology. These were mainly streams and drainage channels with relatively low alkalinity and dissolved mineral concentrations. Although the densities of apple snails in these sites were very low, and it is not sure whether they were transported by water from the surrounding areas when flooding occurred during the summer monsoons, their presence indicates that they could at least survive in these habitats for a period of time. Our observation indicated that they are especially prone to drift in currents during mating. However, it remains to be tested whether apple snails can complete their life cycle in such fast flowing streams. Dudgeon & Corlett (2004) reported that, of the other common species of freshwater gastropods in Hong Kong, only *Brotia hainanensis*, which has a strong foot to hold on to rocks in stream beds, can reproduce to reach substantial densities in such habitats. Apple snails grown in tap water with a Ca^{2+} concentration of 11 mg/L last year in our lab from neonates had thin shells. When the water was supplemented with a small bag of coral fragments, this shell thinning phenomenon disappeared. From the field survey, the lowest Ca^{2+} concentration in the sites where apple snails were present was 9.1 mg/L. These observations indicate the potential limiting effect of calcium and alkalinity, but more data from laboratory controlled experiments and field transplant experiments are required to determine whether the chemical characteristics of the stream water or flow rate is the limiting factor for the distribution of *P. canaliculata*.

Of particular interest was that two sites on Lantau Island that were classified as inhabitable, yet lacked apple snails (Fig. 1). Of these two sites, Pui O is an abandoned paddy field, and Tong Fuk is a cement-lined drainage channel. The gastropods *Melanoides tuberculata* and *Physella acuta* where found in Pui O and Tong Fuk, respectively. Elsewhere in the surveyed area throughout New Territories, these gastropods were often found together with *P. canaliculata*. Such a sympatric distribution pattern indicates that apple snails may share some common habitat requirements with these two freshwater snails, or that they have the same dispersal mechanism (i.e., transported by water in streams and channels). Additionally, the input of nutrients from animals or domestic waste water and other salts associated past agricultural activities, such as calcium in lime, may be the reason for these sites being classified as inhabitable by apple snails in the DFA. Because our data provided evidence that chemical characteristics of the water in these two sites was suitable for the colonization of apple snails, their absence indicates that they have not been introduced into these sites due to geographic isolation.

Implications for Management

Although *P. canaliculata* preferred waters of high levels of alkalinity and nutrients characteristic of vegetable farming areas in northern New Territories, it was still sometimes found in streams with low levels of alkalinity and nutrients. The unsuitable chemical characteristics of the water on Hong Kong Island would prevent apple snails from establishing a population on this island. However, the presence of two sites of favorable chemical characteristics of the water on Lantau Island indicates a possible risk of future colonization by apple snails on this island. It is important to note that, once introduced to favorable habitats, apple snails may spread very quickly, and it is very difficult to eradicate them.

Throughout the study we have emphasized the importance of environmental characteristics that may affect the colonization of apple snails. A recent study has shown that, once colonization has taken place, apple snails can affect the habitat, such as decreasing the biomass of wetland macrophytes and increasing the nutrient contents of the water (Carlsson et al., 2004; Carlsson & Lacoursière, 2005). It can not be excluded that the presence of apple snails may also contribute to water quality and the patterns of PCA and DFA observed in this study. These recent results should also be considered in the management of apple snails. No matter whether the chemical characteristics of the water are apparently unsuitable for apple snails, caution should be taken by the government to prevent the apple snails from spreading to the wetlands of Hong Kong and Lantau Islands where there are macrophytes. This is particularly relevant because a number of wetlands on these islands are being marketed as ecotourism attractions.

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LITERATURE CITED

AFCD [Fisheries and Conservation Department, Hong Kong Special Administrative Region], 2007, Agriculture in Hong Kong. http://www.afcd.gov.hk/english/ agriculture/agr_hk/agr_hk.html [Cited 25 June 2007].

ALDERSON, E. G., 1925, *Studies in Ampullaria*. Cambridge, W. Heffer & Sons. xx + 102 pp.

CARLSSON, N. O. L., C. BRÖNMARK & L.-A. HANSSON, 2004, Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology*, 85: 1575–1580.

CARLSSON, N. O. L. & J. O. LACOURSIÈRE, 2005, Herbivory on aquatic vascular plants by the introduced golden apple snail (*Pomacea canaliculata*) in Lao PDR. *Biological Invasions*, 7: 233–241.

CAZZANIGA, N. J., 2002, Old species and new concepts in the taxonomy of *Pomacea* (Gastropoda: Ampullariidae). *Biocell*, 26: 71–81.

CHA, M. W., 1989, Interspecific interactions among freshwater Gastropoda in Hong Kong.

Unpublished M. Phil. Thesis, Hong Kong Polytechnic, Hong Kong.

CHANG, W. C., 1985, The ecological studies on the *Ampullaria* snails. *Bulletin of Malacology, Republic of China*, 11: 43–51.

COWIE, R. H., 1997, *Pila* Röding, 1798 and *Pomacea* Perry, 1810 (Mollusca, Gastropoda): proposed placement on the Official List, and Ampullariidae Gray, 1824: proposed confirmation as the nomenclaturally valid synonym of Pilidae Preston, 1915. *Bulletin of Zoological Nomenclature*, 54: 83–88.

COWIE, R. H., 2002, Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. Pp. 145–192, in: G. M. BAKER, ed., *Molluscs as crop pests*. Wallingford, New Zealand, CABI Publishing. xii + 468 pp.

COWIE, R. H., K. A. HAYES & S. C. THIENGO, 2006, What are apple snails? Confused taxonomy and some preliminary resolution. Pp. 3–23, in: R. C. JOSHI, ed., *Global advances in ecology and management of golden apple snails*. Muñoz, Nueva Ecija, Philippine Rice Research Institute. x + 588 pp.

DILLON, R. T. Jr., 2000, *The ecology of freshwater molluscs*. Cambridge, Cambridge University Press. xii + 509 pp.

DUDGEON, D. & R. CORLETT, 2004, *The ecology and biodiversity of Hong Kong*. Hong Kong, Friends of the Country Parks / Joint Publishing. 336 pp.

EATON, A. D., L. S. CLESCERI, E. W. RICE, A. E. GREENBERG, eds., 2005, *Standard methods for the examination of water and wastewater*, 21st ed. Washington, D.C., American Public Health Association. Various pagination.

ESTEBENET, A. L. & P. R. MARTÍN, 2003, Shell interpopulation variation and its origin in *Pomacea canaliculata* (Gastropoda: Ampullariidae) from Southern Pampas, Argentina. *Journal of Molluscan Studies*, 69: 301–310.

GREEN, R. H., 1971, A multivariate statistical approach to the Hutchinsonian niche: bivalve mollusks of central Canada. *Ecology*, 52: 543–556.

HALWART, M., 1994, The golden apple snail *Pomacea canaliculata* in Asian rice farming systems: present impact and future threat. *International Journal of Pest Management*, 40: 199–206.

HYLTON-SCOTT, M. I., 1948, Moluscos del noroeste Argentino. *Acta Zoológica Lilloana*, 6: 241–274.

ITO, K., 2002, Environmental factors influencing overwintering success of the golden apple snail, *Pomacea canaliculata* (Gastropoda: Ampullariidae), in the northern most population in Japan. *Applied Entomology and Zoology*, 37: 655–661.

LAM, P. K. S., 1994, Intraspecific life-history variation in *Radix plicatulus* (Gastropoda: Pulmonata: Lymnaeidae). *Journal of Zoology, London*, 232: 435–446.

LODGE, D. M., K. BROWN, S. KLOSIEWSKI, R. STEIN, A. COVICH, B. LEATHERS & C. BRÖNMARK, 1987, Distribution of freshwater snails: spatial scale and relative importance of physiological and biotic factors. *American Malacological Bulletin*, 5: 73–84.

MARTÍN, P. R., A. L. ESTEBENET & N. J. CAZZANIGA, 2001, Factors affecting the distribution of *Pomacea canaliculata* (Gastropoda: Ampullariidae) along its southernmost natural limit. *Malacologia*, 43: 13–23.

MOCHIDA, O., 1991, Spread of freshwater *Pomacea* snail (Pilidae, Mollusca) from Argentina to Asia. *Micronesica, Supplement*, 3: 51–62.

NORUŠIS, M., 2006, *SPSS 15.0 Statistical procedures companion*. Prentice-Hall, Upper Saddle River, New Jersey. xxii + 626 pp.

NAYLOR, R., 1996, Invasions in agriculture: Assessing the cost of the golden apple snail in Asia. *Ambio*, 25: 443–448.

PIZANI, N. V., A. L. ESTEBENET & P. R. MARTIÌN, 2005, Effects of submersion and aerial exposure on clutches and hatchlings of *Pomacea canaliculata* (Gastropoda: Ampullariidae). *American Malacological Bulletin*, 20: 55–63.

TEO, S. S., 2004, Biology of the golden apple snail, *Pomacea canaliculata* (Lamarck, 1822), with emphasis on responses to certain environmental conditions in Sabah, Malaysia. *Molluscan Research*, 24: 139–148.

WADA, T. & K. MATSUKURA, 2007, Seasonal changes in cold hardiness of the invasive freshwater apple snail, *Pomacea canaliculata* (Lamarck) (Gastropoda: Ampullariidae). *Malacologia*, 49: 383–392.

YIPP, M. W., 1990, Distribution of the schistosome vector snail, *Biomphalaria straminea* (Pulmonata: Planorbidae) in Hong Kong. *Journal of Molluscan Studies*, 56: 47–55.

YIPP, M. W., M. W. CHA & X. Y. LIANG, 1991, A preliminary impact assessment of the introduction of two species of *Ampullaria* (Gastropoda: Ampullariidae) into Hong Kong. Pp. 393–397, in: C. MEIER-BROOK, ed., *Proceedings of the Tenth International Malacological Congress, Tübingen 1989*, Baja, Hungary, UNITAS Malacologia, 2 vols. vi + 636 pp.

YUSA, Y., N. SUGIURA & T. WADA, 2006a, Predatory potential of freshwater animals on an invasive agricultural pest, the apple snail *Pomacea canaliculata* (Gastropoda: Ampullariidae), in southern Japan. *Biological Invasions*, 8: 137–147.

YUSA, Y., T. WADA & S. TAKAHASHI, 2006b, Effects of dormant duration, body size, self-burial and water condition on the long-term survival of the apple snail, *Pomacea canaliculata* (Gastropoda: Ampullariidae). *Applied Entomology and Zoology*, 41: 627–632.

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